

Cercopithecoid Locomotion, Support Use, and Support Availability in the Tai Forest, Ivory Coast

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ABSTRACT Habitat heterogeneity is widely theorized to be important in the evolution of Old World monkeys, yet the impact of architecturally distinct forest types on the positional repertoires of African monkeys is largely unknown. As part of a wider project, this study investigates how the locomotor behavior of five sympatric cercopithecoids varies in structurally distinct forest areas. Fieldwork took place in the Tai Forest, Ivory Coast, from June 1993 to August 1994. Data were collected on *Colobus badius*, *C. polykomos*, *C. verus*, *Cercopithecus diana*, and *C. campbelli* ranging throughout a common forest mosaic. The behavior of adult females was sampled using an instantaneous time point scheme at 3 min time intervals. Vegetative differences within each 100 × 100 m grid cell used by all species were quantified. Further, the relative numbers of different sized substrates at 10 m intervals within the canopy were recorded in each cell sampled.

Data indicate that consistency of locomotor behavior across forest types is maintained because most monkeys select the same set of preferred supports in both forest types. The conservative nature of Tai monkey locomotor behavior is discussed within the context of additional proximate and ultimate influences and constraints. © 1996 Wiley-Liss, Inc.

Locomotor behavior observed in the field reflects both *proximate*, or ecology driven influences, and *evolved*, or morphology driven, tendencies (Pounds, 1991). Pounds, a recent critic of locomotor field studies, has taken issue with those who "interpret locomotor variation between species as evidence of adaptation without distinguishing between evolved tendencies and proximate responses or controlling for the latter" (1991:114). To understand fully why animals move the way they do, it is critical to identify those factors which influence locomotor expression given the constraints imposed by anatomy (e.g., Ripley, 1967; Morbeck, 1977; Rose, 1979; Fleagle and Mittermeier, 1980; Crompton, 1984; Cant, 1992; Cannon and Leighton, 1994).

Variation in the size, inclination (i.e., angle), compliance (i.e., flexibility), abun-

dance, and spatial distribution of supports is widely theorized to promote certain types of positional behavior while limiting others (Napier, 1962; Napier and Napier, 1967; Ashton and Oxnard, 1964; Stern and Oxnard, 1973; Charles-Dominique, 1977; Mackinnon and Mackinnon, 1978; Fleagle, 1978, 1979). Thus, the characteristics of supports associated with different locomotor activities are routinely collected in field studies to establish better some predictive relationship between substrates and preferred modes of locomotion (e.g., Fleagle et al., 1981). By demonstrating how an animal's locomotion

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and anatomy are correlated with support use, we may achieve a better understanding of living primates' locomotor ecology, and, by analogy, our inferences about the behavior of extinct primates become more compelling.

Nevertheless, while the goal of many field studies is to establish a functional relationship between a species' locomotor profile and its support use, it is still not entirely clear to what extent the expression of specific locomotor modes depends on specific support types. This may be particularly true for primates, such as most Old World monkeys, who lack more specialized adaptations such as prehensile tails, claws, or morphologies for brachiation or vertical clinging (e.g., see Gebo and Chapman, 1995a). If so, then determining why different sized quadrupedal monkeys locomote at different forest levels can be a fruitful inquiry. For example, if larger arboreal quadrupeds require larger supports on which to run and walk, then these monkeys should tend to move at those forest levels where larger supports are more abundant. When they do not, the issue of support choice becomes of paramount importance.

What happens when a primate is confronted with a different set of supports from which to choose? Do support use and accompanying locomotor behaviors change, or do primates somehow manage to maintain consistency in their patterns of movement and habitat use? These questions have recently received attention, but there is, as yet, a lack of consensus concerning the extent that locomotor behavior is influenced by differences in arboreal architecture. On the one hand, a number of authors have shown that primates readily respond to architectural (i.e., structural) differences as revealed by changes in locomotor frequencies between habitat types (Dagosto, 1992; Gebo and Chapman, 1995b; Walker, 1993). Conversely, others have demonstrated that primates maintain locomotor "equivalence" across habitat types despite significant differences in the spatial arrangements of supports (Cant, 1986; Fontaine, 1990; Garber and Pruetz, 1995). This apparent discrepancy is problematic, particularly if paleoprimatologists rely on living models to infer the behavior of fossil animals. Do these studies imply

that the relationship between primates and their habitats is so context specific that generalizations about ultimate mechanisms are futile? Here I will argue that in order to understand support use it is necessary to have an independent assessment of support availability. By examining the limits, or conversely the flexibility of an animal's positional behavior as well as the extent that animals of different body sizes use specific substrates, it is possible to explain how one group of monkeys responds to habitat heterogeneity.

The purpose of this paper is to examine the locomotion of five Old World monkeys in different architectural contexts where some measure of relative support availability is known. The following questions are asked: 1) Do monkeys maintain similar locomotor profiles across structurally distinct habitats? 2) If not, do changes in locomotor profiles reflect use of different kinds of supports? 3) If yes, are monkeys maintaining similar locomotor profiles by being selective in their support use within the context of different support availability? By addressing these issues, it is possible to determine what effect, if any, structural differences have on the locomotor profiles of a group of different sized monkeys while demonstrating variation in accompanying support use.

PREDICTIONS

Larger arboreal, quadrupedal monkeys will tend to use larger substrates to support their greater weight and better maintain their center of gravity above the support (cf. Napier, 1967; Fleagle, 1980; Fleagle and Mittermeier, 1980; Cartmill, 1985). It follows, then, that smaller monkeys will be able to exploit a wider array of different sized substrates within a given forest. If forest levels are characterized by different sized substrates, then there should be a strong correlation between the forest level at which large monkeys are found and the abundance of larger substrates at that level. The relationship between the forest level at which smaller monkeys are found and the abundance of supports of a particular size should be less consistent because small monkeys

are not similarly constrained by the availability of large supports. Theoretically, when at different forest levels, smaller monkeys will utilize the more abundant supports rather than seek out substrates of a particular size for their pathways.

If larger monkeys are more limited by the size of substrates within each forest type, then these monkeys will show less variation in locomotor frequencies between forest types. This is because large monkeys will be more likely to seek out those strata containing substrates of preferred (i.e., large) size to move in by virtue of the fact that they are more limited by the availability of large substrates. When not at levels dominated by large supports, large monkeys will still tend to seek out larger though less abundant substrates at those levels. For smaller monkeys, a less consistent relationship will exist between the height at which each monkey is found and the abundance of different sized supports at each height due mainly to the capacity of smaller monkeys to utilize a greater variety of supports (e.g., Anapol and Bischoff, 1992).

METHODS

Study site

Data were collected in the Tai National Park, Ivory Coast, from June 1993 to August 1994. The park, located between 6° 20' N to 5° 10' N and 4° 20' W to 6° 50' W is the last remaining major block of rain forest in West Africa consisting of approximately 330,000 hectares (1,600 square miles) of forest. Average annual rainfall is 1,830 mm, and the year is characterized by two wet seasons (July–August and November–February). Mean annual temperature is 24°C. The study site is located near the field station of the Institut de la Ecologie Tropicale (IET) of the Ministère d'Enseignement Supérieur et Recherche Scientifique of Ivory Coast. This research station, on the western border of the park, is approximately 25 km from the Liberian border. The core study area covers approximately 1 km² of moist, evergreen rain forest.

The Tai Monkey Project was started in 1989 by Ronald Noë and Bettie Sluijter. Since then, a number of European students

have worked at habituating groups of each species (except *Cercocebus atys*, which is only partially habituated) while pursuing various projects. When this study began, members of each species were fully habituated. Prior studies on primates in the Tai Forest include the study of Galat and Galat-Luong (1985) and the ongoing chimpanzee project of Boesch (Boesch, 1978, 1994; Boesch and Boesch, 1981, 1983, 1989, 1990; Doran, 1992, 1993a,b).

Locomotor and contextual data

Five monkey species were included in this study: *Colobus polykomos*, or western black and white colobus (8.3 k), *Colobus badius*, or red colobus (8.2 k), *Colobus verus*, or olive colobus (4.2 k), *Cercopithecus diana*, or diana monkey (3.9 k), and *Cercopithecus campbelli*, or Campbell's guenon (2.7 k).¹ Because all monkey groups contained more adult females than males, the former were chosen as focal animals. Female positional behavior was recorded at every 3 min time point, and the same individual was not sampled within 15 min of itself to assure independence of data points. By using females, I was able to sample a greater number of different individuals while not having to wait long periods of time between samples. The 15 min time interval was based on prior analyses of dependency in data (C. Janson, personal communication).

Species were sampled on a rotating, weekly basis. When possible, a species was sampled continuously for approximately 5 days in a row before switching to the next species. Every attempt was made to sample species evenly throughout the length of the study in order to minimize any possible seasonal effect. Each morning, the focal species was located in its sleeping tree and followed all day until a sleeping tree (or location) for that night had been selected. The next morning, I returned to where I had left the focal species and resumed sampling. On those occasions when the previous day's focal species could not be located, I attempted to locate and sample the following week's species.

At every 3 min time point, the following

¹Body weights (adult females) are from Oates et al. (1990).

data were recorded: maintenance activity (i.e., feeding, resting, traveling, foraging²), height in forest (estimated visually in meters), location (grid cell), locomotor behavior, and support type. The recognized locomotor behaviors were quadrupedal walking (slow, quadrupedal pronograde locomotion), quadrupedal running (fast gaits including bounding and galloping), leaping (progression between discontinuous supports using primarily rapid extension of the hindlimbs for propulsion; landing includes both hindlimbs and forelimbs), climbing (vertical ascent in which the arms reach above the head and pull the animal up while the hindlimbs alternatively push the body up), and arm swinging (locomotion involving forelimb suspension: bimanualism) (after Fleagle, 1977a).

Following Fleagle (1976) and Fleagle and Mittermeier (1980), supports were classified as one of three types: boughs (large supports usually greater than 10 cm in diameter in which grasping with hands or feet is not possible), branches (medium sized supports between 2 and 10 cm in diameter permitting grasping of hands or feet), or twigs (small flexible terminal branches usually less than 2 cm in diameter). Although the Tai monkeys do differ in body size, it is doubtful that differences in hand size were great enough to cause incorrect classification of support size via grasping capabilities (e.g., see Biegert, 1963; Schultz, 1970).

Data from transcribed notebooks were analyzed using SAS (SAS Institute Inc., 1985) and BIOM (Rohlf, 1982–1987). The sample sizes (number of 3 min locomotor and postural time points respectively) are *Colobus polykomos* (918, 2,620), *Colobus badius* (1,466, 2,730), *Colobus verus* (507, 1,088), *Cercopithecus diana* (1,553, 1,986), and *Cercopithecus campbelli* (596, 841). The discrepancy between the number of observations is due to the difference in numbers of adult females among species groups.

Dependency of positional behavior data. Various authors have discussed the

problems of data dependency (in time) inherent in positional studies (Mendel, 1976; Janson, 1984, 1990; Walker, 1993; Dagosto, 1994). For example, when continuously sampling species who spend large portions of their day resting in the same position, one risks generating temporally autocorrelated data despite the precautions taken in the chosen sampling regime discussed above. In order to determine if, in fact, the postural data collected during this study were independent (i.e., one observation does not predict the subsequent ones), the frequency that each postural behavior was observed at time one (X) was compared with the frequency that each other postural behavior was observed at time two (X plus 1) for each species. The resulting matrix was then compared to an X^2 distribution to test the null hypothesis that the data are not dependent (i.e., the data are not temporally autocorrelated). Rare postures (those <10) were lumped together and treated as a single behavior to avoid artificially inflating the number of matrix cells and, accordingly, the appropriate critical value.

The critical X^2 values followed by the Williams-corrected G values (Sokal and Rohlf, 1981) for each species were as follows: *Colobus polykomos* (26.296, 16.2192), *Colobus badius* (31.410, 14.2253), *Colobus verus* (21.026, 12.9085), *Cercopithecus diana* (31.410, 2.4701), and *Cercopithecus campbelli* (12.592, .8144). These data reveal that the 3 min time point data were independent: for no species were the postural data-dependent. It is therefore highly unlikely that the locomotor data exhibit dependency, and analyses of each species' total positional behavior data set could then be used without having to divide them into smaller, independent subsets.

Botanical data

Floral survey. Although all primary forest is in a constant state of regeneration (sylvigenesis), natural (e.g., treefalls) and unnatural (e.g., logging) disturbances can often yield large pockets of secondary growth within an otherwise pristine habitat. These phenomena can result in abrupt changes in the structural properties of forest which may, in turn, affect the locomotion of mon-

²Foraging (travel while feeding) includes locomotion during feeding within a single tree and/or between adjacent trees.

keys moving through this habitat mosaic (e.g., Gebo and Chapman, 1995b; but see Garber and Pruetz, 1995). For this reason, sampling of the forest was undertaken at an accordingly fine scale, and grid cells were denoted as type A if the sampling grid fell in an area of forest where no disturbance was recognizable and type B if any type of natural or unnatural disturbance in the forest was included within the sampling rectangle (i.e., tree falls or areas where human disturbance was sufficient to influence the architecture of the forest). Disturbance in these areas is perhaps due to the fact that the core study area is bordered by two major trails as well as an abandoned road. In addition, there is evidence that a few trees were logged from the forest as recently as 10 years ago.

Thirty-six 100×100 meter cells in the study grid were sampled in order to determine the relative abundance of different sized trees. Sampling was conducted in a 20×50 meter rectangle within each grid cell (Fig. 1). The orientation of the rectangle was alternated in adjacent cells in order to reduce the dependency between cells. Placement of the rectangle in the grid cell depended on the orientation (i.e., horizontal or vertical relative to due north) of the sampling plot for that cell. For plots oriented horizontally, the northwest corner of the cell was found (via painted trees), and a distance of 40 m was marched off due south using calibrated steps. From that point, a distance of 25 m due east was measured using a 25 m tape and a compass. This resulting point was the first point of the sampling rectangle. A distance of 50 m was then measured due east of this point. A perpendicular line 20 m in length was dropped due south midway along the 50 m line (at the 25 m position). The end of this line marked the southern border of the rectangle, and 25 m lines were then directed due east and west to form the bottom border, parallel to the northern border. The eastern and western borders were then delineated by connecting the end points of the northern and southern borders. For sampling plots oriented vertically, 40 m were marched off due east (along the northern border of the grid cell), and a distance of 25 m was measured due south. This then

became the first point of the sampling plot, and the remainder of the quadrant's borders were determined accordingly.

All trees greater than 2 m in height and with a diameter at breast height greater than 4 cm were identified (species), their heights measured using a rangefinder, their circumferences at breast height determined using a tape, and their identifications marked with numbered botanical tags. A wooden gauge, 4 cm wide, was fashioned to more quickly determine if the tree required measuring. In addition, all trees greater than 2 m in height but with diameters less than 4 cm (i.e., saplings) were counted in one-half of the sampling plot.

For trees straddling the borders of the sampling plot, the tree was considered in the plot if the middle of the stem at breast height was within the sampling quadrant. In cases of doubt, a coin was flipped. The circumference of multitemmed trees was determined by summing the areas of all stems (the area of each stem was determined using each stem's circumference to figure its radius, calculating the radius of the total circle, and then determining the circle's circumference using the equation $2\pi r$). The height of multitemmed trees was recorded as the highest point of any stem. For trees with large buttresses in which it was impossible to record diameter at breast height, the circumference was measured (or estimated) directly above the buttress. Lianas were measured only once per individual and at the thickest part at breast height (or whatever could be reached as close as possible to that). Dead and nearly dead (e.g., some green leaves were still present) trees were marked as such, and the height of the tree was measured from the ground to its greatest altitude, regardless of whether the highest support was dead or alive.

Canopy survey. Canopy surveys were conducted to obtain an estimate of the relative abundance of different sized substrates at different heights throughout the study area. Sampling of the vertical structure was undertaken at six points within each grid cell (Fig. 2). These points were determined using a sampling template, and the orientation of this template was alternated in adjacent

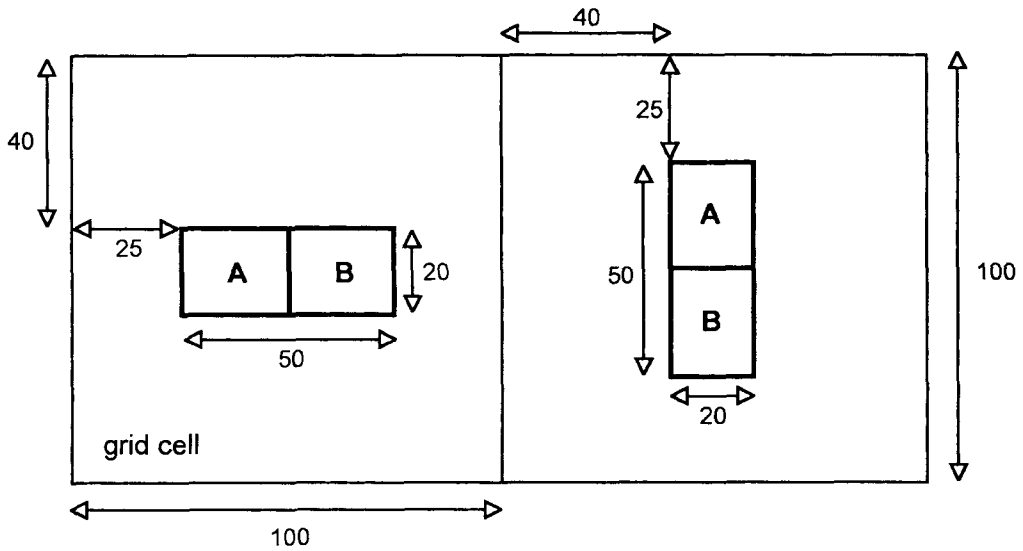


Fig. 1. Orientations and dimensions of sampling plots for floral survey. All distances are in meters.

cells to reduce the dependency between cells. Placement of the sampling template within the grid cell and all distances between sampling points were determined using a 50 m tape. All sampling points were at least 20 m apart. This distance, the estimated maximum width of a tree crown, was chosen to ensure that the samples are independent and that the same tree was not sampled consecutively. A standard rangefinder was used to survey the canopy directly above each sampling plot. Aiming the rangefinder straight up, the height of the tallest substrate was recorded and its diameter estimated. This substrate served as a focal point around which the sampling field was delineated; all supports in the same plane within 3 m of the marker support were counted and their type noted. Sampling continued at descending 10 m intervals until the field surrounding the lowest substrate was measured. Thus, the number of canopy classes (10 m samples) varied depending on the height of the tree(s) being sampled. In those instances when a support obstructed my view to greater altitudes, I adjusted my position so that a clearer line of sight was available to the higher forest levels. Every effort was made to keep the sampling fields in the

same vertical as well as horizontal planes. Zero values were recorded for intervals in which no measurable substrates were found. Skills at estimating substrate number and diameters were refined by practicing in forest areas where the numbers and diameters can be measured precisely.

Data from the canopy survey were analyzed using a three factor log linear model with two forest types, five height classes, and three types of supports (Sokal and Rohlf, 1981). This model is used with frequency data and tests for the interaction among three or more factors.

RESULTS

Botanical results

Data from the botanical survey reveal that the undisturbed forest (type A) contained fewer total stems (7,786) than did the disturbed forest (9,068). Undisturbed forest contained 2,345 trees and 5,531 saplings, while trees and saplings numbered 2,885 and 6,183 respectively in disturbed forest.

Results of the canopy survey are presented in Table 1. The significant Williams-corrected G value for interaction implies that there are pairwise associations between all

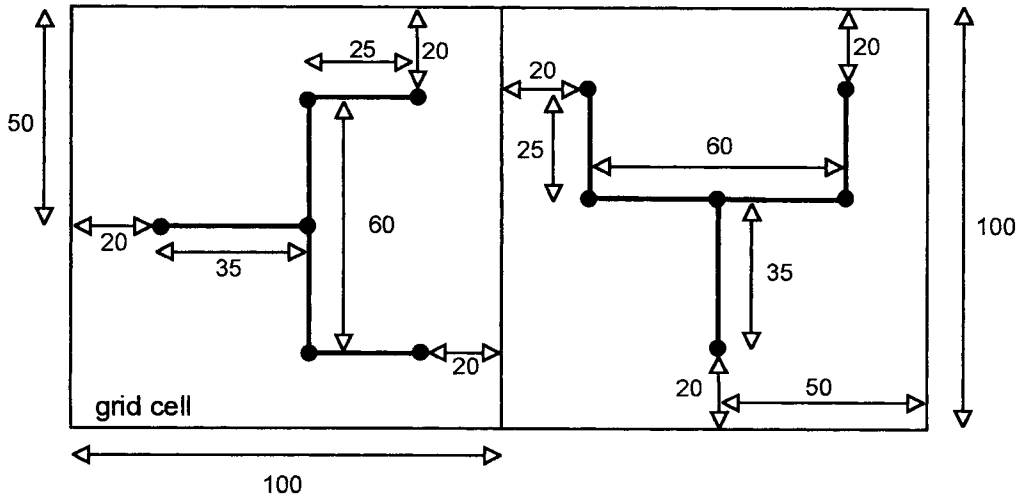


Fig. 2. Orientations and dimensions of sampling templates for canopy survey. All distances are in meters.

of the three factors (forest type, height, and support type). Analysis of all pairwise comparisons reveals a significant result in each case: most notably, the number of different support types at each forest level differs significantly in each forest type. That is, the forest types differ not only in the relative number of supports at each level but also in the types of supports at each level. Disturbed forest (type B) is generally more dense at lower levels with higher numbers of twigs and branches and fewer boughs. Undisturbed forest (type A) has fewer total supports but more boughs at all levels. For example, between 11 and 20 m, undisturbed forest has nearly three times the number of boughs despite having half as many total supports.

Locomotor results

Table 2 summarizes each species' locomotor activity (i.e., locomotor profile) in the two forest types. The data, also displayed in Figure 3, demonstrate that locomotor frequencies of all species were remarkably consistent across the forest types. Examination of the Williams-corrected G values revealed no significant differences in the overall locomo-

TABLE 1. Distribution of supports in two forest types¹

Forest type A (Undisturbed)				
Height	Bough	Branch	Twig	Total
>40	—	29	85	114
31–40	58	200	429	687
21–30	127	264	582	973
11–20	108	295	626	1,029
0–10	26	374	607	1,007
Total	319	1,162	2,329	3,810
Forest type B (Disturbed)				
Height	Bough	Branch	Twig	Total
>40	—	7	48	55
31–40	13	156	314	483
21–30	101	427	748	1,276
11–20	35	503	1,526	2,064
0–10	13	827	1,031	1,871
Total	162	1,920	3,667	5,749

¹Data are summed frequencies of each support type at each 10 m interval. Three factor (forest type, height, support type) log-linear model of support differences: Interaction: G(Williams) = 70.328 (significant) (critical χ^2 value (.05) = 15.507). See text for discussion.

tor profiles of each species across the two habitats. The largest difference for any monkey was a 5.9% change in leaping by *Colobus polykomos*. These results do not imply, of course, that there are not important differences between species. Indeed, the test for conditional independence which examines

TABLE 2. Locomotor profiles¹ in each forest type

Species	Forest type A (Undisturbed)				
	AS	CL	L	QR	QW
<i>Colobus badius</i>	4.9	17.6	16.9	6.9	53.6
<i>Colobus polykomos</i>	0	13.3	9.2	32.6	44.9
<i>Colobus verus</i>	0	11.7	21	21	46.4
<i>Cercopithecus diana</i>	0	18.1	9.7	11.8	60.4
<i>Cercopithecus campbelli</i>	0	14.1	5	7.8	73

Species	Forest type B (Disturbed)				
	AS	CL	L	QR	QW
<i>Colobus badius</i>	3.3	16.7	18.4	8.9	52.8
<i>Colobus polykomos</i>	0	14.4	15.1	29.2	41.4
<i>Colobus verus</i>	0	12.3	19.9	24	44.1
<i>Cercopithecus diana</i>	0	20.6	11.1	9.9	58.4
<i>Cercopithecus campbelli</i>	0	15.1	5.4	7.5	72

¹Data under each column are the percentages of total locomotor time that each locomotor behavior was observed. AS, arm swing; CL, climb; L, leap; QR, quadrupedal run (including bound); QW, quadrupedal walk. Statistical analyses pertaining to this table are discussed in the text. Briefly, the findings were as follows:

Species	G(Williams): (Interforest locomotion)	Critical X ² value	N
<i>Colobus badius</i>	4.6318 (ns)	9.488 (.05)	1,466
<i>Colobus polykomos</i>	7.0164 (ns)	7.815 (.05)	918
<i>Colobus verus</i>	6.7270 (ns)	7.815 (.05)	507
<i>Cercopithecus diana</i>	3.4403 (ns)	7.815 (.05)	1,553
<i>Cercopithecus campbelli</i>	4.1495 (ns)	7.815 (.05)	596

Test of conditional independence: G(Williams) = 659.547. Significant. Three-factor interaction: G(Williams) = 26.055. Not significant.

the significance of the differences between species yielded a very large Williams-corrected G value (659.547). This test reveals there are considerable differences in the locomotion of all species both within and between forests (McGraw, 1996). Nevertheless, the nonsignificant result from simultaneous consideration of all three factors (species, locomotion, and forest type) indicates that, taken together, the locomotor profiles of all five monkeys did not change significantly across forest types.

Despite the lack of statistical differences, for most species there are trends in the direction that three behaviors changes across forest types: all species walked less in disturbed forest (type B), all species except *Colobus badius* climbed more in forest type B, and all species except *Colobus verus* leaped more in forest type B.

Overall support use. Tables 3 through 7 and Figure 4 show the frequency that each support type at each forest level was used by each species across the two forest types. In order to determine whether species were consistent in their support use across forest types, it is first necessary to test for interac-

tion of all three variables (support type, height, forest type). If the resulting G value (which tests for the partial association between each combination of paired variables) is not significant, we must nevertheless subsequently test for conditional independence. In this case, we are concerned whether support types (factor A) at different heights (factor B) were used in similar proportions given two forest types (factor C).

For three of the five species, *Colobus badius*, *C. verus*, and *Cercopithecus campbelli*, neither the three-way interaction nor the test for conditional independence was significant. For *Cercopithecus diana*, the three-way interaction was significant, although the test for conditional independence was not (G(Williams) = 11.488). Thus, although there is a significant interaction between all three variables (forest type, height, and support type), the actual supports used by *C. diana* did not differ across forest types. For *Colobus polykomos*, the three-way interaction test was not significant, while the Williams-corrected G value derived from the test of conditional independence (13.065) exceeded, although barely, the critical X² value

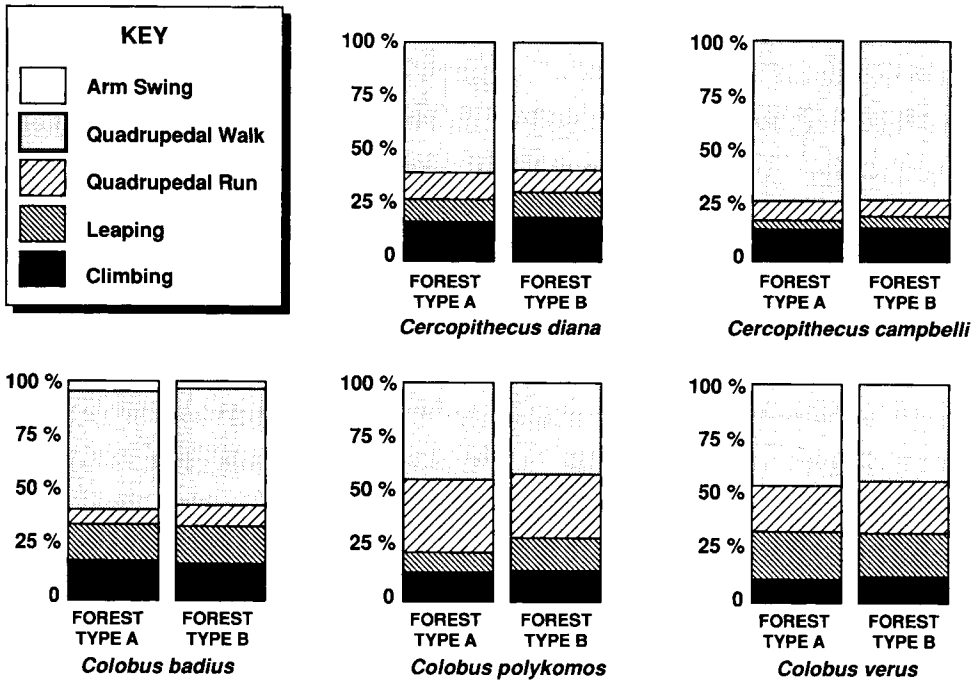


Fig. 3. Locomotor data on five monkeys in two forest types. Analysis revealed no statistical differences between habitats (see Table 2).

TABLE 3. Support use¹ at each height interval in each forest type: *Colobus badius*

Height interval	Forest type A		
	Bough	Branch	Twig
>40	50	33.3	16.7
31-40	49	25.1	26.3
21-30	39	29.7	31.2
11-20	24	33.6	43
0-10	—	—	—

Height interval	Forest Type B		
	Bough	Branch	Twig
>40	50	21	29
31-40	52	23	25
21-30	40	29	31
11-20	20	35.5	44.5
0-10	—	—	—

¹Data represent the frequency that each support type was used at each 10 m interval. Three-factor interaction: $G(\text{Williams}) = 1.330$ (ns) (critical $X^2 = 12.592$); test of conditional independence: $G(\text{Williams}) = 1.665$ (ns) (critical $X^2 = 15.507$). See text for discussion.

TABLE 4. Support use¹ at each height interval in each forest type: *Colobus polykomos*

Height interval	Forest type A		
	Bough	Branch	Twig
>40	—	—	—
31-40	53	27	20
21-30	48	29	23
11-20	34	38	28
0-10	—	—	—

Height interval	Forest type B		
	Bough	Branch	Twig
>40	—	—	—
31-40	58	20	22
21-30	46	31	23
11-20	19	38	43
0-10	—	—	—

¹Data represent the frequency that each support type was used at each 10 m interval. Three-factor interaction: $G(\text{Williams}) = 9.214$ (ns) (critical $X^2 = 9.488$); test for conditional independence: $G(\text{Williams}) = 13.065$ (* = significant [.05]) (critical $X^2 = 12.592$). For discussion, see text.

(12.592). The data indicate that between 11 and 20 m *C. polykomos* used fewer boughs and more twigs in disturbed forest. Support use by this monkey at the remaining forest

levels was generally consistent across forest types. Thus, in four (and nearly all) of the five cases, the monkeys used the same overall supports in the two forest types.

TABLE 5. Support use¹ at each height interval in each forest type: *Colobus verus*

Height interval	Forest type A		
	Bough	Branch	Twig
>40	—	—	—
31–40	—	—	—
21–30	44.4	35.2	20.4
11–20	19.6	49.7	30.7
0–10	8	44	48

Height interval	Forest type B		
	Bough	Branch	Twig
>40	—	—	—
31–40	—	—	—
21–30	56	31	13
11–20	18.3	37.2	44.5
0–10	9	64	27

¹ Data represent the frequency that each support type was used at each 10 m interval. Three-way interaction: G(Williams) = 6.052 (ns) (critical χ^2 = 9.488); test for conditional independence: G(Williams) = 11.018 (critical χ^2 = 12.592). For discussion, see text.

TABLE 6. Support use¹ at each height interval in each forest type: *Cercopithecus diana*

Height interval	Forest type A		
	Bough	Branch	Twig
>40	—	—	—
31–40	30	30	40
21–30	28.7	37.4	33.9
11–20	17.6	36.6	45.8
0–10	8.7	43.5	47.8

Height interval	Forest type B		
	Bough	Branch	Twig
>40	—	—	—
31–40	27.5	34.5	39.8
21–30	31.4	28.3	40.3
11–20	11.7	41.9	44.7
0–10	—	—	—

¹ Data represent the frequency that each support type was used at each 10 m interval. Three-way interaction: G(Williams) = 9.687 (* = significant [.05]) (critical χ^2 = 9.488); test for conditional independence: G(Williams) = 11.488 (ns) (critical χ^2 = 12.592). For discussion, see text.

Bough use. In general, boughs were used most often by larger monkeys. At most levels and in both forest types, *Colobus badius* and *C. polykomos* were the most frequent users of boughs, although these large supports never comprised more than 58% of the total supports these monkeys used at any level. When all height intervals across forest types are compared, the maximum number of boughs used at any one interval ranged between 20% and 50% for *Colobus badius* and 19% and 58% for *Colobus polykomos*. *Colobus verus* displayed an even greater disparity in

TABLE 7. Support use¹ at each height interval in each forest type: *Cercopithecus campbelli*

Height interval	Forest type A		
	Bough	Branch	Twig
>40	—	—	—
31–40	—	—	—
21–30	—	—	—
11–20	14.8	47.5	37.7
0–10	9.4	54.7	35.9

Height interval	Forest type B		
	Bough	Branch	Twig
>40	—	—	—
31–40	—	—	—
21–30	—	—	—
11–20	11.6	51.4	37
0–10	19.3	43.9	36.8

¹ Data represent the frequency that each support type was used at each 10 m interval. Three-way interaction: G(Williams) = 4.198 (ns) (critical χ^2 = 5.991); Test for conditional independence: G(Williams) = 7.991 (ns) (critical χ^2 = 9.488). For discussion, see text.

bough use across height intervals and forest types: boughs comprised 8% of the supports used between 0 and 10 m in forest type A compared to 56% between 21 and 30 m in forest type B. Maximum bough use ranged between 8.7% and 31.4% in *Cercopithecus diana* and between 9.4% and 19.3% in *C. campbelli*.

Branch use. Larger monkeys (*Colobus badius* and *C. polykomos*) used branches less often than smaller monkeys. When all height intervals across forest types are compared, the maximum use of branches at any one interval was comparatively low for red colobus (21–30%) and for black and white colobus (20–38%) at any given forest level. Once again, *Colobus verus* displayed the greatest disparity in branch use at any one height interval, with a low of 31% between 21 and 30 m and a high of 64% between 0 and 10 m in forest type B. *Cercopithecus campbelli* was very consistent in its use of branches, with a range between 44% and 55% across all heights in both forest types. Branch use in *C. diana* varied more, ranging between 28% and 44% within a single height interval.

Twig use. When all height intervals across forest types are compared, colobus monkeys displayed the greatest variability in use of twigs. Maximum twig use at any one interval ranged between 16.7% and 45% in *Colobus badius* and between 20% and 43% in *C. poly-*

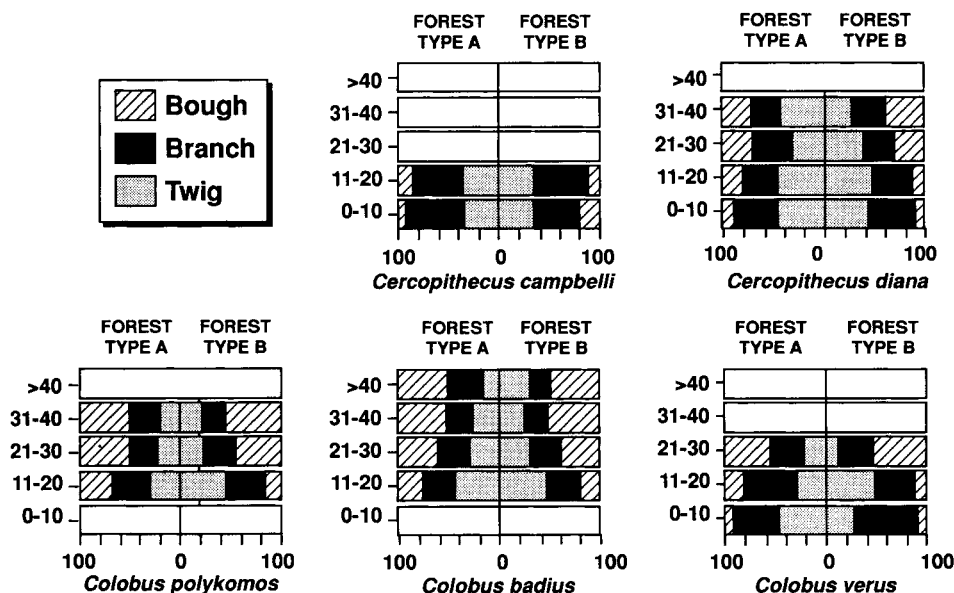


Fig. 4. Support use of five monkeys across two forest types. Analysis revealed that only *Colobus polykomos* showed a significant difference in support use between habitats (see Tables 3–7).

komos. The olive colobus exhibited the greatest difference (between 13% and 48%). In contrast, the guenons were more consistent in their use of fine supports: use of twigs at any one interval in *Cercopithecus diana* ranged between 33.9% and 47.8% across forest levels and height intervals, while use of twigs by *C. campbelli* varied little, between 35.9% and 37.7%.

Review of predictions

It was predicted above that larger monkeys would use the largest supports most often and would frequent those strata where large supports tend to be concentrated. In general, large monkeys are the most frequent users of large supports, and in most cases (across all height intervals and both forest types) boughs are the most frequently used support of large monkeys. For *Colobus badius* and *C. polykomos*, boughs were the most preferred support in every height interval except between 11 and 20 m in both forest types. The red colobus and the black and white colobus spent approximately 80% of their locomotor time in the main canopy (between 21 and 40 m) (Table 8). Boughs are most common between 21 and 30 m in both

forest types but much less so between 31 and 40 m, particularly in forest type B. Therefore, it does appear that although bough use is highly variable between forest intervals, large monkeys do use locomotor routes at altitudes where boughs are most common, though relatively scarce.

It was predicted that smaller monkeys, able to use a wider variety of supports, would be less restricted in their canopy use. *Cercopithecus diana* tended to use all forest levels more evenly in both forests and demonstrated the most catholic use of supports. Nevertheless, it is interesting to note that boughs were the most frequently used supports at only one height interval across forest types. In every other case, the most frequently used supports were twigs. Although support use of the diana monkey was less restricted to a single support type, this monkey appeared to use twigs most often which are the most common supports at all forest levels across forest types.

In contrast to the similarly sized diana monkey, *Cercopithecus campbelli* locomoted in a much narrower forest zone (20 m and below) and was much less diverse in its support use. Boughs are relatively scarce below

TABLE 8. Proportion of time spent locomoting¹ within each ten meter interval in two forest types

Species	Forest type A				
	Ground-10	11-20	21-30	31-40	+40
<i>Colobus badius</i>	.54	19.9	47.8	30.6	1.1
<i>Colobus polykomos</i>	1.1	15.7	41.6	40.6	1.1
<i>Colobus verus</i>	11	68.3	18.3	2.4	0
<i>Cercopithecus diana</i>	5.4	41.7	34.8	17.7	.4
<i>Cercopithecus campbelli</i>	35.6	57.8	5	1.6	0

Species	Forest type B				
	Ground-10	11-20	21-30	31-40	+40
<i>Colobus badius</i>	.3	15	42.3	39	3.2
<i>Colobus polykomos</i>	1.1	13.7	38.5	44.1	2.6
<i>Colobus verus</i>	15.3	59.8	20.7	4.2	0
<i>Cercopithecus diana</i>	5.1	46.2	28.2	18.9	1.6
<i>Cercopithecus campbelli</i>	42.1	51.1	5.1	1.8	0

¹ Data under each column are the percentages of total locomotor time that each locomotor behavior was observed.

20 m and, while they were used less frequently than any other support type, boughs were still used in proportions far greater than their availability. *C. campbelli* showed the most consistency (i.e., least variation) in support use across forest types, and branches were always the most frequently utilized support.

Support and canopy use in *Colobus verus* are the most difficult to interpret. In general, canopy use is consistent across forest types (between 60% and 68% of all locomotion took place between 11 and 20 m). The olive colobus does tend to use more boughs as forest height increases; however, there is no consistent pattern to branch and/or twig use at different heights and in different forest types. It is therefore difficult to state convincingly what kinds of supports the olive colobus prefers.

The predictions concerning which monkeys would be more or less likely to change their locomotor profiles across forest types were not upheld, as the differences in support availability across the forest types did not affect the locomotor behavior of any monkey enough to cause a significant change.

DISCUSSION

These results demonstrate that despite differences in the structural properties of the two forest types, the locomotor profiles of these five Old World monkey species are remarkably consistent across the two habitats. How is locomotor consistency maintained across habitats? The data suggest that

rather than making use of supports in proportions similar to their availability, most monkeys choose the same set of supports. That is, similar frequencies of climbing, leaping, and quadrupedalism are achieved because most monkeys use a consistent distribution of support types independent of variation in the abundance of support types across habitat types. The most notable examples are the similar frequencies with which larger monkeys (*Colobus badius* and *Colobus polykomos*) use boughs despite their differential availabilities.

In certain cases, the correlation between supports chosen for locomotion within different height intervals can, of course, be related to the relative paucity or abundance of particular support types at particular levels. However, with only a few exceptions, supports were not used in proportions similar to their availability. The largest monkeys, *Colobus badius* and *C. polykomos*, frequently use large supports at most forest heights and in both forest types although they were always the most scarce substrate available. *Cercopithecus campbelli*, the smallest monkey, did not use twigs most frequently at any height but rather used medium sized supports in all contexts and used boughs at much higher frequencies than their abundance would predict. Except for the increased use of boughs as forest height increased, there was little consistency or pattern in the support use exhibited by *Colobus verus*. Only the use of twigs by *Cercopithecus diana* was done with frequen-

cies approaching this support types abundance.

Considering these differences, the relative uniformity of locomotor behavior across forest types is all the more remarkable. Although there were trends in the direction that some behaviors changed across forest types, these data emphasize both the conservative nature of each species' locomotor profile as well as (in four and nearly all cases) the consistency with which a fixed profile of supports is used. While the locomotor profiles do not reflect proximate differences in habitat structure, the similarity in observed locomotor behavior implies that some underlying set of factors, other than body size, operates to limit, or conversely, determine behavior. For example, within any given array of supports, a small bodied primate has a much greater choice of stable substrates on which to move than a large bodied primate. We would therefore expect large bodied arboreal quadrupeds to concentrate their locomotion on large supports, while smaller primates used a greater variety of supports. Analysis of support use reveals that while each species uses a specific subset of supports, all monkeys can nevertheless use all kinds of supports. That they do not, to a greater degree, suggests additional constraining factors.

Various authors have offered both speculation and quantitative demonstration of the determinants of locomotor behavior. As locomotor field studies have become more refined both in their methodological approach as well as in the nature of their questions, there is now little doubt that observed behavior is the combined product of body size (Fleagle and Mittermeier, 1980; Susman et al., 1980), morphology (Fleagle, 1977a,b; Hunt, 1991; Anapol and Bischoff, 1992; Doran, 1993a), foraging requirements (Gautier-Hion et al., 1981; Boinski, 1989; Janson and Boinski, 1992; Garber, 1992; Biccamarques and Calegario-Marques, 1993), predation risk (Gebo et al., 1994), seasonality (Gebo and Chapman, 1995b), ontogeny (Doran, 1992), sex (Cant, 1987; Doran, 1993b), maintenance activities (Fleagle, 1980; Hunt, 1992), and polyspecific associations (Isbell, 1991; Gebo, 1992) and that even simultaneous consideration of multiple fac-

tors may still not predict an animal's locomotion beyond gross behavioral patterns. This is best seen when differences in habitat do not consistently yield differences in locomotion.

These findings support those of Garber and Pruetz (1995), among others, who argued that primate locomotor behavior—at least as far as habitat is concerned—is highly conservative. At the same time, however, these conclusions are counter to those of Gebo and Chapman (1995b), who documented differences in the locomotor behavior of red colobus monkeys in Uganda. What explanations can be offered?

First, it is possible that the habitat differences at Tai were simply not sufficient to warrant a significant change in locomotion; the disturbed areas of forest may still retain enough "primary structure" to permit unaffected locomotion. Second, even if this were not the case and the structural differences in support availability are biologically meaningful, it is possible that the density of different sized supports may not even be the relevant variable when examining the locomotion of quadrupedal monkeys. A more important consideration for monkeys seeking to straighten path lengths between points (Cant, 1992) may be those canopy pockets where supports are entirely absent (i.e., gaps). Other investigators have successfully quantified this habitat feature and even constructed a model for predicting canopy use based on gap data (Cannon and Leighton, 1994). Clearly, identifying the structural properties most responsible for determining arboreal locomotion is only one of the important tasks facing primatologists. Accurately quantifying these properties will undoubtedly be even more challenging. Nevertheless, only after we have a better understanding of how the structural properties of habitat influence locomotion can we begin to assess why the locomotor behavior of some primates is more variable than others.

Understanding why animals move the way they do is a multivariate problem. Body size alone, for example, can go only so far in predicting both support and general canopy use. In the case of the Tai monkeys, it appears that some combination of factors is

ultimately responsible for overriding the proximate differences in habitat structure and yielding a conservative positional repertoire. These data suggest that while different sized monkeys may frequently use one type of support more than others, it may be more useful to think of primates as using a fixed profile of supports as dictated by individual foraging, physiological, anatomical, and ecological needs and constraints.

CONCLUSIONS

First, these results corroborate previous findings that positional behavior is highly conservative in many primate taxa. The locomotor profiles of five monkeys observed in the Tai Forest change little when a species moves from one forest type to another. Despite differences in the structural properties of two forest types, the overall locomotor profiles of each species are remarkably similar across these habitat types.

Second, in the case of four (and nearly all) of five Tai monkeys, locomotor equivalence across habitat types at some level appears to be maintained by active selection of a subset of supports. This is best seen in the larger monkeys who use larger supports in similar proportions across habitat types despite their differential availability. Even smaller monkeys appear to maintain substrate fidelity rather than make use of more abundant supports.

Third, these data have implications for interpreting the behavior of fossil monkeys. While we may be able to infer gross locomotor patterns of fossil monkeys using analogies from living animals, the conservative nature of these patterns may make reconstructing accompanying habitats more difficult.

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